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# Tidal growth patterns and growth curves of the Miocene potamidid gastropod *Vicarya yokoyamai*

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**Abstract. Continuous growth sequences are recorded in vertical (= median longitudinal) sections of the columella of the fossil potamidid gastropod *Vicarya yokoyamai* Takeyama, from subtropical Miocene faunas of Japan. Shells from the Mizunami, Uchiura, Bihoku, and Masuda groups show semidiurnal tidal growth patterns. This suggests that *V. yokoyamai* lived in the intertidal zone. Growth curves were reconstructed on the basis of numbers of tidal growth lines. These growth curves were found to be very similar with one another, and indicated that shell-height increased from 1.5 cm to 8 cm in two years.**

**Key words : columella, growth rate, intertidal, micro-growth increment, micro-growth line, tide**

## Introduction

Invertebrate hard parts such as molluscan shells and coral skeletons grow incrementally, forming alternating sequences of micro-growth lines and micro-growth increments that constitute their micro-growth patterns. Micro-growth patterns reflect physiological and environmental changes that occurred during their formation. Reconstruction of these changes from micro-growth patterns observed in the hard parts of a variety of organisms has been attempted in many studies (e.g. Wells, 1963 ; Berry and Barker, 1968 ; House and Farrow, 1968 ; Pannella and MacClintock, 1968 ; Pannella *et al*., 1968 ; Dolman, 1975 ; Scrutton, 1978 ; Lutz and Rhoads, 1980 among others).

Intertidal organisms such as bivalves, gastropods, and barnacles record the effects of changing tides, as exposure and immersion are commonly reflected in their micro-growth patterns (Evans, 1972 ; Bourget and Crisp, 1975 ; Crisp and Richardson, 1975 ; Richardson *et al*., 1979, 1980a, 1980b, 1981 ; Richardson *et al*., 1980c ; Ekarante and Crisp, 1982 ; Ohno and Takenouchi, 1984 ; Ohno, 1984, 1985, 1989 ; Richardson, 1987, 1988a, 1988b ; Tojo and Ohno, 1999). Using these records, ancient tidal periods and tidal patterns have been reconstructed from fossil bivalves (Ohno, 1984, 1989 ; Tojo *et al*., 1999). Tidal growth patterns are also a suitable index for the time scale of growth, so they can be used to reconstruct the growth rates of hard parts (Richardson, 1987 ; Tojo and Ohno, 1999). Previous studies of growth rates are based in many cases on annual rings that were recognized by comparative analysis of growth lines and oxygen isotopes of the shells (Jones *et al*., 1978 ; Jones, 1980 ; Thompson *et al*., 1980 ; Jones, 1981), but many gastropods have no obvious yearly rings. Thus we attempt the reconstruction of growth curves from tidal growth patterns.

Few studies of micro-growth patterns in gastropod shells have been undertaken, because coiling of the gastropod shell obstructs the collection of continuous growth sequences spanning the whorls. However, Tojo and Ohno (1999) have proposed an easy method to obtain a continuous micro-growth pattern from one whorl to the next in the Recent potamidid gastropod *Terebralia palustris* (Linnaeus), using sections of the columella. This method made it easy to access records of gastropod growth. Tojo and Ohno (1999) observed tidal growth patterns in shells of *T. palustris*. They inferred that one micro-growth line corresponds to a 12.4 hour interval of low tides and reconstructed the growth curve of an individual *T. palustris* shell. This growth curve was consistent with one that had been reconstructed from a population analysis. Analysis of micro-growth patterns by this method permits the reconstruction of changing growth rates even from a single fossil specimen or species known only from small populations.

The fossil potamidid gastropod *Vicarya* has been regarded as a characteristic element of warm-water faunas from Eocene to Miocene in age. Tojo and Sakakura (1998) reported tidal growth patterns in shells of *Vicarya yokoyamai* from the Mizunami Group. However, little is known of the growth of *Vicarya* because it is an extinct genus.

The method of Tojo and Ohno (1999) can be applied to shells of *V. yokoyamai*. We observed tidal growth patterns in shells of *V. yokoyamai* from four localities (Figure 1) and reconstructed their growth curves.

## Material

In this study, we used fragments of *V. yokoyamai* from

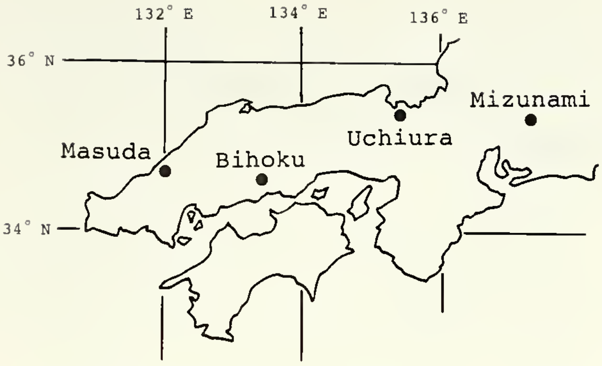


**Figure 1.** Locality map for *Vicarya yokoyamai* specimens utilized in this study.

subtropical tidal or shallow marine facies of Miocene age in Japan. To reconstruct the growth curve of *V. yokoyamai* (Figure 2A), we used a total of six specimens, three from the Mizunami Group in Gifu Prefecture, and one each from the Uchiura Group in Kyoto Prefecture, the Bihoku Group in Okayama Prefecture, and the Masuda Group in Shimane Prefecture (Figure 1). In the following discussion, specimens are referred to by the group name, and the three specimens from the Mizunami Group are called Mizunami A, B and C. Two species names that had been established, *V. yokoyamai* and *Vicarya japonica*, were synonymized by Kanno (1986).

## Preparation for columella method

In order to prepare vertical (=median longitudinal) and horizontal (=cross) sections of the gastropod shell, samples were cut and ground with a graded series of carborundum and polished with diamond paste. A binocular microscope and a scanning electron microscope (SEM) were used for observation of shell micro-growth patterns (Figure 2B). For observation with the SEM, polished samples were etched with 0.5 mol/l HCl and then coated with gold.

## Results

### Micro-growth pattern

Micro-growth pattern consists of two components of growth layers, micro-growth lines and micro-growth increments. Micro-growth lines are the layers which are relatively resistant to etching. Thus, they are observed as liner-ridges under SEM. Micro-growth increments are the layers between micro-growth lines. Micro-growth lines show various thicknesses, but are generally thinner than micro-growth increments.

Micro-growth lines of *V. yokoyamai* appear as relatively light layers under the binocular microscope (Figures 2B, D).

### Formation of columella

Before observing the columella sections, we examined the outer shape of the columella to understand its formation (Figure 2C). The basal part of the columella has a trough-like structure along its coiling axis. One flank of the trough continues to the outer lip; the other covers the bottom of the preexisting whorl (Figure 2C). During growth of the shell, the trough extends downwards (abapically) in the direction of coiling, the apical end being filled with new shell material. The formation of new growth layers over this surface results in the formation of the columella.

Growth layers at the bottom of the trough contribute to growth of the central part of the columella, and those on the preexisting outer surface of the neck contribute to growth of the columella rim and a part of a whorl. This layer becomes part of the "ceiling" of the new shell whorl. The new shell is laid down directly upon that formed in the previous whorl. This surface of contact appears as a line in shell sections that is referred to as the "borderline" (Figures 2B, D; Tojo and Ohno, 1999).

### Appearance of the growth layers in sections

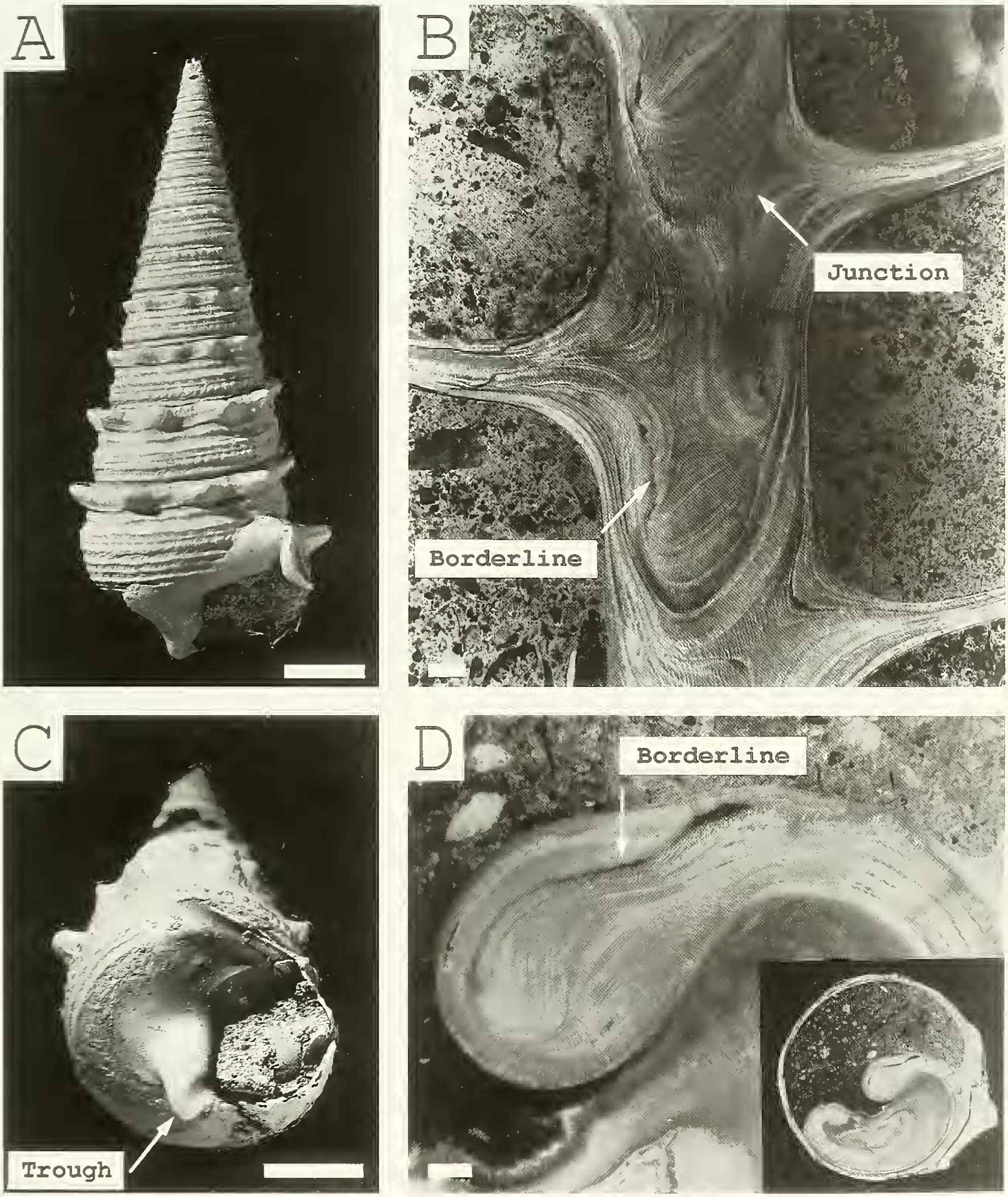
In vertical (=median longitudinal) section, each whorl shows a pair of more or less hyperbolic patterns, alternately on the right and left sides of the coiling axis (Figures 2B, 3). One is the trace of the trough facing the observer, and the other is that of the trough opposing the observer. The center of this hyperbolic pattern is called the "junction" (Figure 2B; Tojo and Ohno, 1999). The shell of the columella between successive junctions on the same side of the coiling axis corresponds to the growth record of one shell whorl. Borderlines are also observed in vertical sections (Figure 2B).

### Continuous growth sequence on the vertical shell section

Correlation of the growth layers was accomplished by tracing them on vertical (=median longitudinal) and horizontal (=cross) sections. First a vertical section was made and the growth layers on it were documented (Figure 2B). Then the two halves of the shell were glued together with adhesive. The "repaired shell" was then cut horizontally. The cut surface was polished and its growth layers were documented (Figure 2D). Then the surface was ground away until shell corresponding to 90° of coiling had been removed. Polishing and documentation of horizontal sections at 90° intervals was repeated for more than one full whorl of the shell (Figure 3).

The columella occupies the center of the cross section,

**Figure 2.** **A**. A shell of *Vicarya yokoyamai* Takeyama, Middle Miocene, Mizunami Group, Gifu Pref. The scale bar is 1cm long. **B**. A vertical section of *Vicarya yokoyamai*, Middle Miocene, Mizunami Group, Gifu Pref. Along the coiling axis, micro-growth lines and intervening micro-growth increments are observed. The scale bar is 1mm long. **C**. The basal part of columella of *Vicarya yokoyamai*, Middle Miocene, Mizunami Group, Gifu Pref. The trough running along the columella and the new shell layer covering the previous whorl surface can be seen. The scale bar is 1cm long. **D**. A horizontal section of *Vicarya yokoyamai* with the columella at the center, Middle Miocene, Mizunami Group, Gifu Pref. The scale bar is 1mm long. (Photomicrographs of sections taken with binocular microscope.)


A
B
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C
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D
Borderline

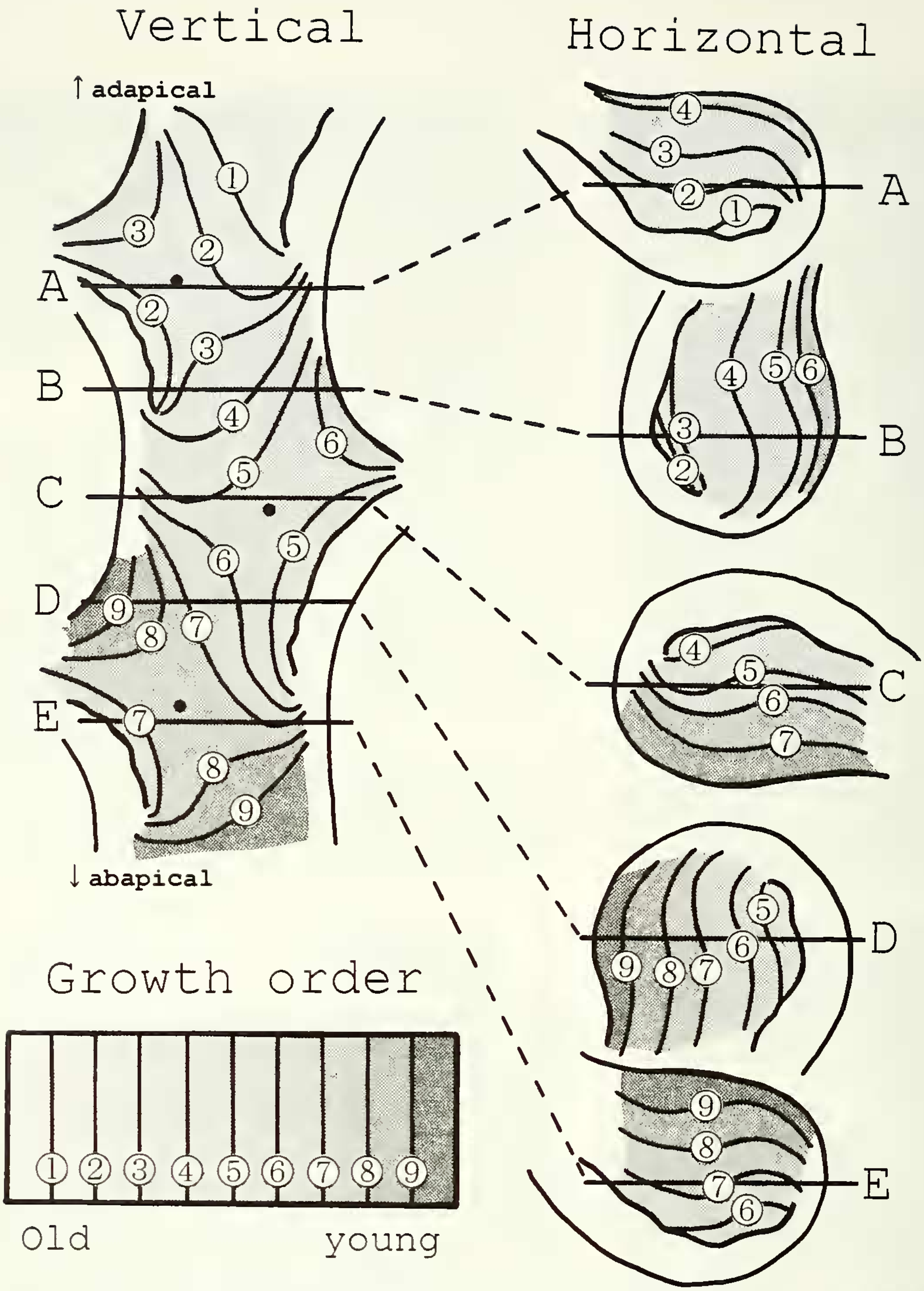

**Figure 3.** Correlation of growth layers on vertical (= median longitudinal) sections and horizontal (= cross) sections. Growth layers are numbered in temporal order from 1 to 9. Lines A to E show the correspondence of vertical and horizontal sections. On vertical section dots show junctions.

with a portion of the whorl extending away from it as if it were a vortex (Figure 2D). One side of the link between the columella and the vortex forms a concave surface and the other side is convex. The concave surface is underlain by an accumulation of numerous U-shaped layers. In successive horizontal sections, viewed abapically, the vortex rotates clockwise. New growth layers are added to the surface of the concave side, move to the convex side abapically, and

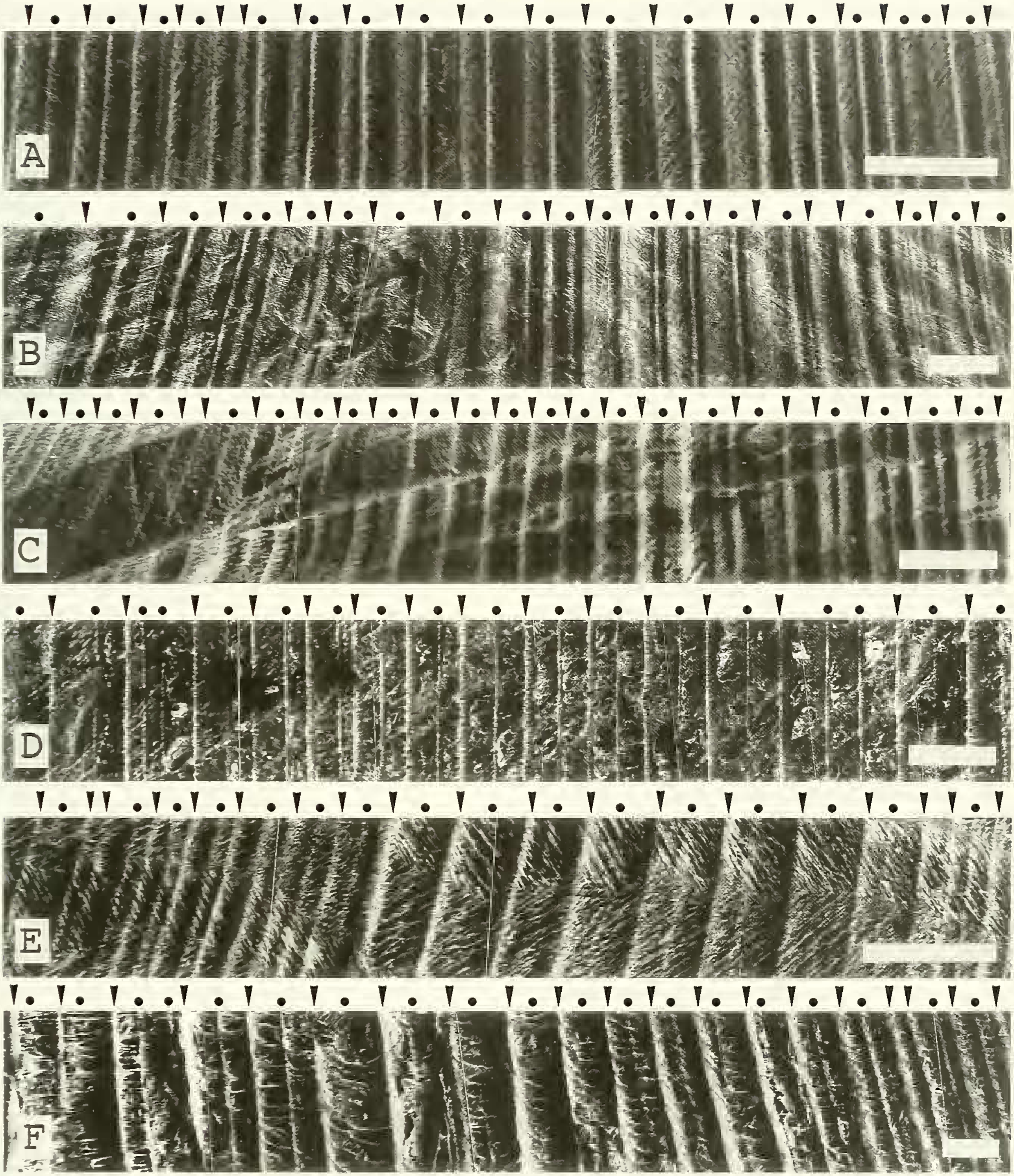

**Figure 4.** Tidal growth patterns recorded in the columella sections of *Vicarya yokoyamai*. **A**. Mizunami A specimen. **B**. Mizunami B specimen. **C**. Mizunami C specimen. **D**. Uchiura specimen. **E**. Bihoku specimen. **F**. Masuda specimen. Continuous semidiurnal tidal growth patterns are indicated by the alternation of thicker (arrowhead) and thinner (dot) micro-growth lines. The order of micro-growth line thickness changes. All scale bars represent 100 $\mu$m. (Photomicrographs taken with SEM.)

finally vanish.

Through observation of successive horizontal sections at 90° intervals the growth layers could be examined and numbered. In Figure 3 (right) the stack of numerous U-shaped growth layers is shown diagrammatically. Only lines with characteristic features, which could easily be correlated in vertical and horizontal sections, were numbered; the oldest conspicuous growth layer was numbered 1 and the newest numbered 9. All the corresponding growth layers could be seen on the vertical section for this growth interval, corresponding to more than one shell whorl (Figure 3 left). Since the mode of growth of the *V. yokoyamai* shell does not change during its ontogeny, all visible growth layers can be recognized and counted on the median longitudinal section of the shell.

## Tidal growth patterns

*Vicarya yokoyamai* shells from the four localities show two sorts of accretionary patterns of micro-growth lines on the columella (Figure 4). One is the alternation of thicker (indicated by arrowheads in Figure 4) and thinner (dots in Figure 4) micro-growth lines. The other is an inversion of the arrangement of thicker and thinner micro-growth lines at approximately every 28.5 growth lines. The same micro-growth patterns of *V. yokoyamai* were reported in specimens from the Mizunami Group by Tojo and Sakakura (1998). These are characteristic features of tidal growth patterns (Dolman, 1975; Richardson *et al.*, 1979, 1980a, 1981; Richardson, 1988b; Ohno, 1989).

Identical alternations and inversions are reported from intertidal bivalves (Richardson *et al.*, 1979, 1981; Ohno, 1984, 1989; Richardson, 1988b) and gastropods (Ohno and Takenouchi, 1984; Tojo and Ohno, 1999). In bivalve shells from semidiurnal, mesotidal regimes, the alternation of thicker and thinner micro-growth lines is caused by differences in temperature between daytime and nighttime exposures to the air (Richardson *et al.*, 1980a; Richardson 1988b; Ohno, 1989). Inversions in the order of thicker and thinner micro-growth lines result from the different periodicities of approximately semidiurnal tides and of the 24 hour cycle of day and night. The zone where the inversion occurs is called the "switch zone" (Ohno, 1989). This mechanism may be responsible for the alternations and inversions observed in the succession of micro-growth lines of *V. yokoyamai* (Figure 4) from the Middle Miocene. This result is compatible with the tidal growth patterns of fossil bivalves from the Mizunami Group recognized by Ohno (1989). The preservation of this micro-growth pattern in all specimens suggests that *V. yokoyamai* lived in the intertidal zone.

The relationship between the number of tidal emersions and micro-growth lines in intertidal bivalves and gastropods has been confirmed by several experiments (Richardson *et al.*, 1979, 1980a, 1980b; Richardson *et al.*, 1980c; Ekarante and Crisp, 1982; Ohno, 1983, 1985, 1989; Richardson, 1987, 1988a, 1988b). Hence, it is reasonable to infer that one micro-growth line in the shell of *V. yokoyamai* is formed in each tidal cycle.

## Reconstruction of growth curves

A continuous growth record can be obtained from the vertical section of a columella (Figures 2, 3). If shell growth was semidiurnal in *V. yokoyamai*, it should be possible to reconstruct growth curves using these observations.

### Height of shell

To reconstruct the growth curve of *V. yokoyamai*, we had to estimate the original height of the shell. However, all specimens had lost some part of the apical portion of the shell. We extrapolated to determine the original height from the angle defined by the whorls of the surviving shell (Figure 5).

### Growth curves of Mizunami specimens

We counted the number of micro-growth lines and measured the shell height at which each junction between whorls of the Mizunami specimens was formed (hereafter called junction height: Figure 5). The shell between successive junctions on the same side of the coiling axis corresponds to the growth record of one shell whorl. Therefore, the number of micro-growth lines between successive junctions, multiplied by 12.4 hours, represents the

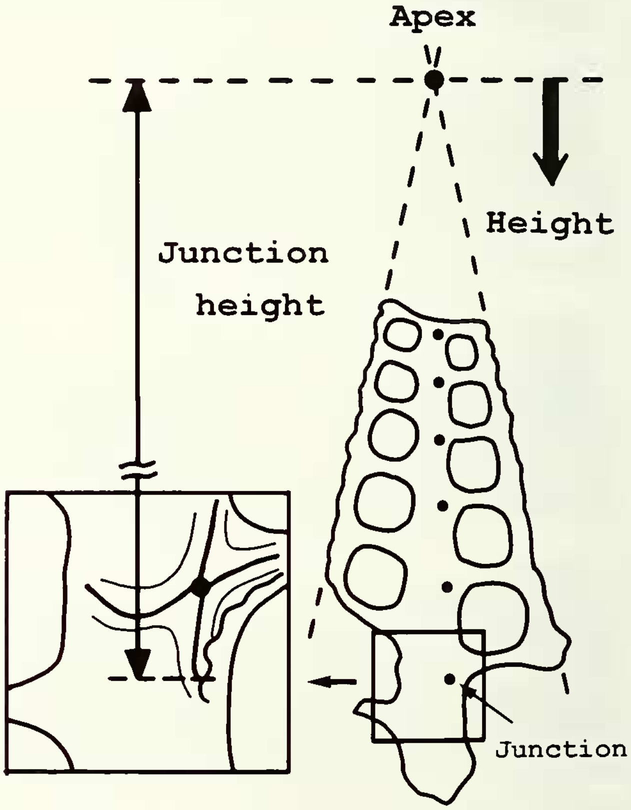

**Figure 5.** Shell height is the vertical distance between the tip of the columella and the reconstructed position of the apex, extrapolated from the outer surface of surviving shell whorls. Junction height is the shell height at which each junction was formed.

time required for growth of the shell whorl. Given the junction heights, we were able to reconstruct the growth curve.

First, the data for Mizunami C were plotted on a graph (Figure 6A). Then, data for Mizunami A and B were plotted as if their first junction heights lined up with that of Mizunami C (Figure 6A). The points plotted are based on the total number of clear micro-growth lines plus half the number of unclear micro-growth lines. Error bars represent the accumulated number of unclear micro-growth lines. This graph shows that the growth curves of Mizunami specimens are similar. The growth rate gradually decreased with growth.

### Growth curves of other specimens

We counted the numbers of micro-growth lines and

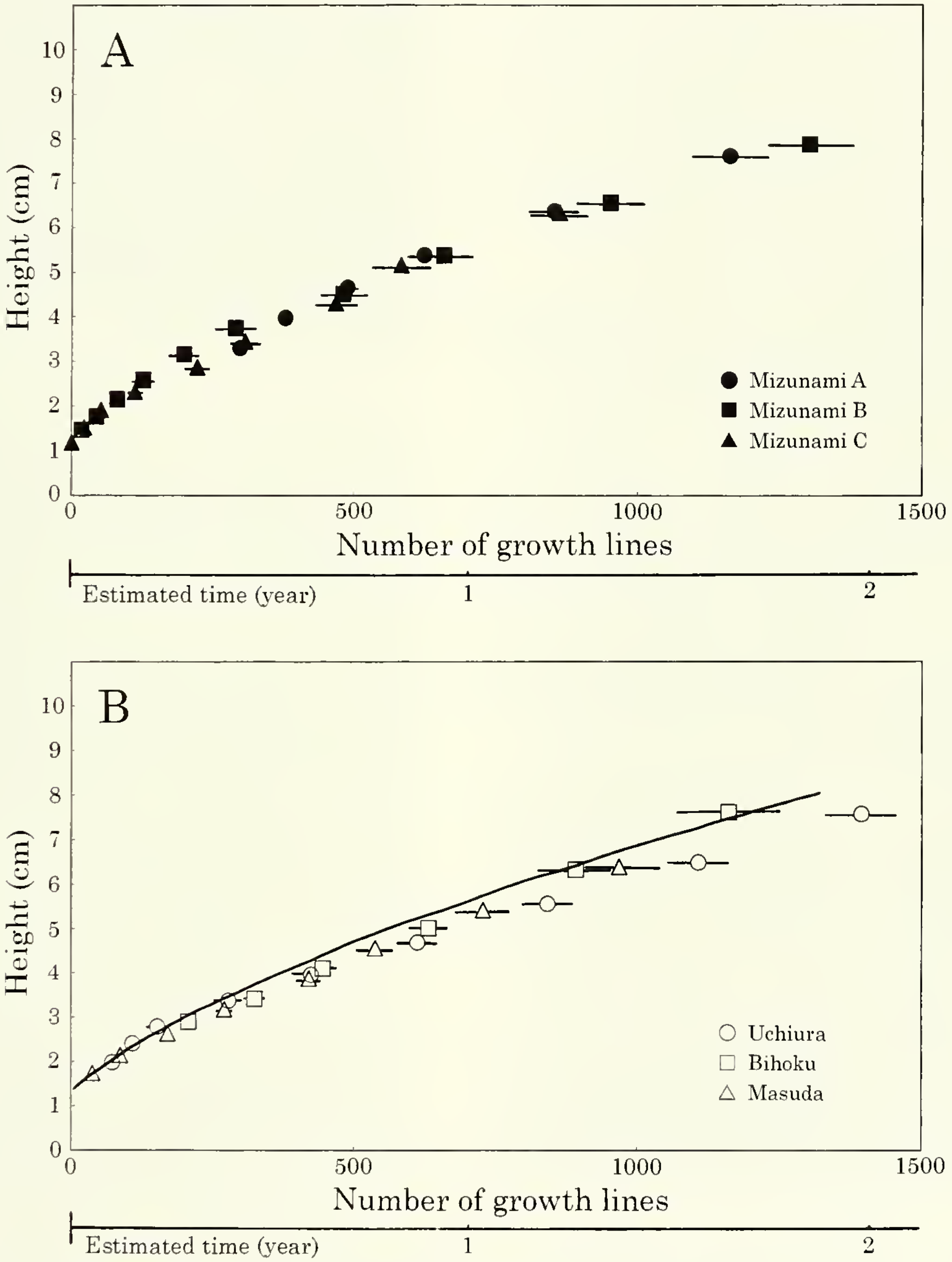

**Figure 6.** **A**. Reconstructed growth curves of *Vicarya yokoyamai* from the Mizunami specimens. **B**. Reconstructed growth curves of *Vicarya yokoyamai* from various areas. The solid line is the approximate growth curve of the Mizunami specimens.

measured the junction heights of other specimens, plotting similar growth curves (Figure 6B). In the figure, the solid line is the curve of best fit to the Mizunami specimen data. Data from other specimens were plotted so that their first junction heights lie on the Mizunami curve (Figure 6B). This graph shows that the growth curves of the Uchiura, Bihoku, and Masuda specimens are similar to those of shells from Mizunami.

## Discussion

Previous studies have suggested that *Vicarya* lived in the intertidal zone of a subtropical mangrove swamp (Oyama, 1950 ; Chinzei, 1978 ; Itoigawa and Tsuda, 1986). This inference is corroborated by the pattern of tidal growth documented here. The alternation of thicker and thinner micro-growth lines is reported only from intertidal organisms. The observation of such alternations in all specimens suggests that *V. yokoyamai* lived in an intertidal zone where it was emersed twice a day.

Distinct major growth breaks, such as winter or spawning breaks, were not observed in this study. This is consistent with the subtropical habitat of *V. yokoyamai*, which lived during the warm Neogene climatic optimum (Chinzei, 1978 ; Chinzei, 1986 ; Ozawa *et al*., 1995). Hence, there was no necessity for a winter break in growth.

We reconstructed the growth curves of six specimens from continuous growth records and the assumption that one micro-growth line formed in a tidal interval. Reconstructed growth curves approximate a logistic form. The logistic pattern of declining growth rate is typical of most invertebrates, indeed of most animals. This suggests the reconstruction is correct. The shells grew from 1.5 cm to 8 cm in height over two years. The adult shell of *Vicarya* has a prominent, thick outer lip. The growth curves suggest that these animals reached maturity and formed the prominent outer lip at the age of two years.

Jones (1981) showed that the standardized growth rate of *Spisula solidissima* changes drastically in conjunction with monthly average mean sea surface temperatures. The change of growth rate is largely explained by the presence of the winter break. In contrast to this cool-water species, the reconstructed growth curves of the *Vicarya* specimens show no or weak seasonal fluctuations. This suggests that *V. yokoyamai* grew in a stable subtropical environment without any climatic deterioration. This inference should be tested by studies of the growth of cooccurring fossils.

The number of specimens studied here is small, due to weathering and recrystallization of most specimens. However, the good agreement of the growth curves in shells from different formations and localities suggests that the columella-method and tidal growth analysis can be used to infer high-resolution population dynamics of fossil gastropod assemblages of various ages.

## Conclusion

The columella method yields evidence of continuous growth sequences in shells of the fossil potamidid gastropod *V. yokoyamai*. The tidal growth patterns of *V. yokoyamai* shells suggest that this gastropod lived in the intertidal zone, under the influence of semidiurnal tides. The reconstructed growth curves of specimens from the Mizunami, Uchiura, Bihoku, and Masuda groups show that their shells grew at similar rates, from 1.5 cm to 8 cm in height in two years.

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